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Recruitment, growth and population size structure of *Pollicipes pollicipes* in SW Portugal

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ABSTRACT

A general model for the life cycle of *Pollicipes pollicipes* in SW Portugal is proposed integrating results from a study on recruitment, growth and population size structure. A brief summary of literature concerning *Pollicipes* published since Margaret Barnes' review paper of 1996 is presented.

Recruitment of *P. pollicipes* on conspecifics (number of cyprids and juveniles with Rostro-Carinal length (RC) <0.6 mm per adult) was intense during summer and autumn, but inter-annual variation in the timing and duration of recruitment season was observed. Different indices of recruitment used in Iberian studies were compared. Spatial correlation between shores (~40 km apart) in SW Portugal suggests that cyprids of *P. pollicipes* are being affected by the same larval pool and physical transport processes operating at this scale. Recruitment of *P. pollicipes* in SW Portugal was higher on the low shore (~2.5 times) than on the high shore. Most recruits were attached to the lower half of the adult peduncle. The period of maximum attachment of juveniles (RC<12.5 mm) to conspecifics was summer and autumn (average of 15 juveniles per adult), while spring was the season with a lower number of juveniles growing on adults (average of 2 juveniles). Size of juveniles attached to conspecifics was rarely greater than 6 mm RC.

Individual annual growth rate of *P. pollicipes* that settled on a denuded surface was 15.7 mm RC (individuals ≤ 1 year old) which corresponds to a monthly increment of 1.3 mm RC in their first year of life.

Size structure analyses of *P. pollicipes* attached directly to primary substratum and/or to the base of conspecifics showed that barnacles at the low tide level reached a higher maximum size, indicating that growth at this level was faster than on the high shore. A higher temporal variability between these size-frequency distributions was detected in spring (March to May). In March, two cohorts (<1 year old, >1 year old) were identified. In May and August, it was difficult to identify individual different cohorts. From mid autumn to early spring, as a consequence of recruitment of barnacles to the primary substratum, it was again possible to identify two cohorts.

1. Introduction

Margaret Barnes (1996) published an extensive review on "Pedunculate cirripedes of the genus *Pollicipes*". Most of this review concerned the European *Pollicipes pollicipes* and the north eastern Pacific *P. polymerus* because very little was known about the tropical eastern Pacific *P. elegans*. More than ten years later, little has been published on *P. elegans* although several studies have been made on *P. pollicipes* (e.g. Kugele and Yule, 1996, 2000; Cruz and Hawkins, 1998; Cruz and Araújo, 1999; Molares and Freire, 2003; Macho et al., 2005; Bald et al., 2006; Borja et al., 2006a; Borja et al., 2006b), although much information remains in unpublished Ph.D. theses (e.g. Cruz, 2000; Pavón, 2003; Macho, 2006) (see Table 1). In this paper, we briefly review the literature on *Pollicipes* published after 1996 (Table 1), and present and re-analyse information regarding recruitment, growth and population size structure of *P. pollicipes* in SW Portugal originally presented in Cruz (2000).

P. pollicipes is a cirripede distributed in Western Europe and on the North African coasts of the eastern Atlantic from Brittany (France) to Senegal, being rare in the Mediterranean (Barnes, 1996). This species is abundant on very exposed rocky shores, ranging from the shallow subtidal to mid-intertidal zone.

Of all species of the genus *Pollicipes*, *P. pollicipes* is the most heavily exploited by man. In Spain and Portugal, it is highly prized as food (1 kg can cost up to 150 Euros in Iberian restaurants). *P. pollicipes* forms clumps of different sizes that are frequently damaged by human harvesting. Considering its vertical intertidal distribution, observations made on the Portuguese coast suggest that exploitation intensity is higher in the low shore than in the mid shore.

P. pollicipes is a simultaneous hermaphrodite, breeding more intensively from April to September on SW Portugal (Cruz and Hawkins, 1998). Brooding patterns differ between size classes and are similar

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Table 1
Studies about the genus Pollicipes published since the review by Barnes (1996). References are given in chronological order. IJ — international journal; Rep — report; PhD — PhD thesis; CP — conference proceedings; and BC — book chapter.

Reference	Subject	Location	Type of publication
Kugele and Yule (1996)	Larval morphology of *P. pollicipes*	Laboratorial conditions	IJ
Cruz and Hawkins (1998)	Reproduction of *P. pollicpes*	SW Portugal	IJ
Cruz and Araújo (1999)	Reproduction of *P. pollicipes*	SW Portugal	IJ
Jamieson et al. (1999)	Review on the biology of *P. polymerus*	W Canada	Rep
Lauzier (1999a)	Review on the biology of *P. polymerus*	W Canada	Rep
Lauzier (1999b)	Framework for *P. polymerus* fishery	W Canada	Rep
Cruz (2000)	Reproduction, recruitment, growth and size-structure of *P. pollicipes*	SW Portugal	PhD
Kugele and Yule (2000)	Active relocation of *P. pollicipes*	Laboratorial conditions	IJ
Jamieson et al. (2001)	Evaluation of community structure of *P. polymerus* beds	Vancouver Island, Canada	Rep
Lessard et al. (2003)	Fishery of *P. polymerus*	W Canada	CP
Marchinko and Palmer (2003)	Morphology, feeding of *P. polymerus*	Vancouver Island, Canada	IJ
Molares and Freire (2003)	Management of *P. pollicipes*	Galicia, Spain	IJ
Pavón (2003)	Reproduction, recruitment and population dynamics of *P. pollicipes*	Asturias, Spain	PhD
Borja et al. (2004)	Distribution of *P. pollicipes*	Basque Country, Spain	Rep
Castro (2004)	Exploitation of *P. pollicipes*	SW Portugal	PhD
Candeias (2005)	Feeding of *P. pollicipes* larvae	Laboratorial conditions	PhD
Macho et al. (2005)	Larval release of *P. pollicipes*	Galicia, Spain	IJ
Tapia (2005)	Larval distribution of *P. polymerus*	Southern and Baja California	PhD
Bald et al. (2006)	A system dynamics model for the management of *P. pollicipes*	Gaztelugatxe marine reserve, Spain	IJ
Borja et al. (2006a)	Relationship between wave-exposure and biomass of *P. pollicipes*	Gaztelugatxe marine reserve, Spain	IJ
Borja et al. (2006b)	Protection of *P. pollicipes* in a MPA	Gaztelugatxe marine reserve, Spain	IJ
Jesus (2006)	Management and exploitation of *P. pollicipes*	SW Portugal	BC
Macho (2006)	Reproduction, recruitment and larval distribution of *P. pollicipes*	Galicia, Spain	PhD
Quinteiro et al. (2007)	Genetics of *P. pollicipes*	Europe and west Africa	IJ
Campo et al. (2010)	Genetics of *P. pollicipes*	Europe and west Africa	IJ
Jacinto et al. (2010)	Fishery of *P. pollicipes* in a MPA	Nature reserve of Berlengas, Portugal	IJ

across tidal levels (Cruz and Araújo, 1999). Individuals apparently produce asynchronous broods and the estimates of the annual number of broods per individual vary from 1 to 4 (Cruz and Araújo, 1999).

Embryo development occurs inside the mantle cavity of adults until hatching of stage I nauplii. There are six naupliar stages and a cypris stage. The total embryo and larval development time of *P. pollicipes* in the laboratory under controlled conditions is about 1.5 to 2 months (Molares et al., 1994a; Molares et al., 1994b; Kugele and Yule, 1996).

1.1. Settlement and recruitment

Cyprids of *Pollicipes* settle heavily on conspecifics and so recruitment can be monitored with relative ease (Hoffman, 1989; Barnes, 1996). Size distributions of juvenile *P. polymerus* on adult peduncles were studied by Hoffman (1984) and he found that juveniles were not randomly distributed. There was a gradient from the smallest and most abundant near the growth zone (the narrow zone between capitulum and peduncle) to the largest and fewest located near the base of the peduncle. Cyprids or spat attached on the capitulum of an adult were rare. Hoffman (1984) suggested that juveniles could have a limited mobility that enables them to move in the direction of the primary substratum. Active relocation of juvenile *P. pollicipes* along the stalk was confirmed by Kugele and Yule (1993, 2000). According to these authors, the mechanism of relocation is the result of production of new tissue by the mitotically active basal region of the stalk (Chaffee and Lewis, 1988), which may be distorted by high haemolymph pressure into the direction of travel, and of secondary secretion of cement.

Besides conspecifics, recruitment on other surfaces (e.g., crevices and algal mats) has been observed in *P. polymerus* (Bernard, 1988). After six weeks, the great majority of these recruits had disappeared probably due to predation by crabs and polychaetes. Recruitment onto conspecifics helps to create a benign habitat with reduced physical and biological stresses (Bernard, 1988, Satchell and Farrell 1993, Barnes 1996). Differences in settlement and post-settlement mortality of *Pollicipes* on conspecifics versus other substrates have never been tested in the field.

Data on the temporal variability of recruitment of *P. pollicipes* on Iberian shores can be found in De la Hoz and Garcia (1993) (Asturias, Spain) and Molares (1994) (Galicia, Spain) and in unpublished theses (Cruz, 2000 — SW Portugal; Pavón, 2003 — Asturias, Spain; Macho 2006 — Galicia, Spain). However, different types of indices of recruitment were used in these studies: number of cyprids and juveniles of different sizes attached to adults (De la Hoz and Garcia, 1993; Cruz, 2000, Pavón, 2003); and percentage of adults with attached barnacles (Molares, 1994) or juveniles (Macho, 2006).

1.2. Growth and population size structure

Most studies of growth have been of *P. polymerus* (see review of Barnes, 1996) describing growth rates of a small number of marked individuals in certain habitats and conditions (e.g. Lewis and Chia, 1981; Page, 1986) or by following growth of barnacles that have recruited on cleared surfaces (e.g. Hoffman, 1989).

Several studies have demonstrated the potential for variability in rates of growth of barnacles as a function of intertidal location (e.g. Barnes and Powel, 1953). Sanford and Menge (2001) observed a dramatic variation of growth rates of intertidal barnacles (*Balanus glandula* and *Chthamalus dalli*) at a variety of spatial and temporal scales that appeared to be positively correlated with a complex set of oceanographic conditions, including wave exposure, abundance of planktonic food and water temperature.

Despite the economical importance of *P. pollicipes* in Iberia, essential information regarding the variability of growth rate of this species is still lacking.

Population size structure reflects recruitment, growth and mortality rates within a population. These processes are affected by several biological (e.g. larval supply, food, competition, predation and facilitation) and physical factors (e.g. desiccation stress, wave-exposure and sea water temperature). Page (1986) compared the population structure of *P. polymerus* at an intertidal rocky headland and at an offshore oil platform on one occasion, and found differences in the size-frequency distributions that were interpreted as a consequence of differential growth and survival rates between the two sites.

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In order to gain insight on the general recruitment patterns of *P. pollicipes* in SW Portugal, we compare two different types of recruitment measures from Iberian recruitment studies. Additionally, we re-analyze data originally presented by Cruz (2000) for this species and region to address the following questions: 1) What is the recruitment period?, 2) Is recruitment higher in the growth zone of the peduncle?, 3) Does intensity of recruitment vary vertically in the intertidal and between shores?, and 4) Is recruitment spatially correlated between two shores (about 40 km apart)? Furthermore, we describe the temporal variability of population size-structure for *P. pollicipes* at two different intertidal levels on two shores in SW Portugal. Additionally, we present estimates of growth rates obtained for several individuals that recruited onto a cleared surface over a 1-year period. Based on our results and on additional information from Cruz (1993) and Cruz and Araújo (1999), we propose a life cycle model for *P. pollicipes* in SW Portugal.

2. Methods

2.1. Study sites

Two very exposed rocky headlands in SW Portugal were studied: Cabo de Sines (37° 57′53″N, 8° 52′56″W) and Cabo Sardão (37° 36′25″N, 8° 49′2″W) (Fig. 1). These shores were separated by about 40 km. At each shore, two vertical levels were considered: high that corresponds to the middle/upper of *P. pollicipes* intertidal distribution (~+1.5 m to 3 m above MLWS); and low that corresponds to the lower intertidal level of its distribution (~MLWS to +1.5 m).

2.2. Recruitment

From November 1990 to March 1992, approximately 50 adults (RC > 12.5 mm, Cruz and Araújo, 1999) were fortnightly (when possible) and randomly taken from aggregates distributed on both shores and tidal levels. Additional dates were sampled in the high level of Cabo de Sines: October 1990, and from July to October 1992.

An index of recruitment was defined as the number of cyprids plus juveniles with <0.6 mm RC (recruits) that were attached to each adult barnacle (IR06). Based on size-frequency distributions, the estimated age of recruits was less than 15 days. All adults were measured (RC) with callipers of 0.1 mm precision. Using a dissecting microscope, all recruits attached to each adult were counted and allocated to 5 different zones of the adult barnacle: zones A, B, C and D corresponded to quarters of the peduncle, starting with A at the base; whereas zone E corresponded to the capitulum This procedure was followed with samples taken from both tidal levels at Cabo de Sines.

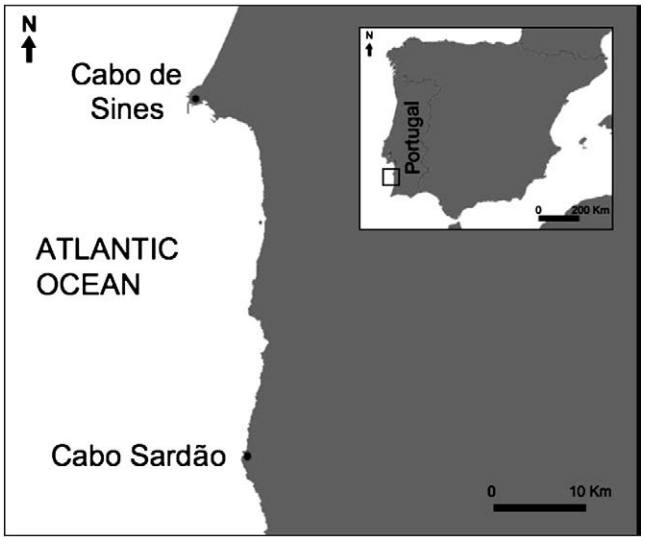

Fig. 1. Map of study sites.

Spatial correlation of recruitment (mean IR06) between both tidal levels within a shore, and between shores for each tidal level was quantified using Pearson correlation coefficients.

In order to compare the results of this study with those obtained by Pavón (2003) and Macho (2006), we have calculated two additional indices of recruitment from the samples taken at Cabo de Sines: the number of cyprids plus juveniles with <1 mm RC that were attached to each adult barnacle (IR1), as used by Pavón (2003); and the percentage of adults with attached juveniles with <1 mm RC (PR1), as used by Macho (2006). Pearson correlation coefficients were quantified between indices (mean IR1 versus mean IR06; mean IR1 versus PR1).

The hypotheses of differential recruitment (IR06) between tidal levels and between shores were tested using analysis of variance with 3 orthogonal factors: tidal level (fixed with two levels — high and low); shore (fixed with two levels — Cabo de Sines and Cabo Sardão); and date (random with four levels that correspond to four dates sampled during the main period of recruitment — July to October 1991). Sample size was 48.

The hypothesis of differential recruitment among zones of the adult was tested for Cabo de Sines using analysis of variance. Due to potential problems of lack of independence among the samples, the dependent variable was the percentage of recruits within a zone relative to the other zones, using 10 randomly chosen and independent animals for each zone. Two orthogonal fixed factors were considered: tidal level (with two levels — high and low); and zone (with five levels — A, B, C, D and E). Six dates during the recruitment season were the replicates ($n=6$).

All analyses of variance were done according to Underwood (1997), using GMAV5 for Windows software (Institute of Marine Ecology, University of Sydney). Homogeneity of variance was assessed using Cochran's C test and SNK tests were used when appropriate (Underwood, 1997).

2.3. Growth and population size structure

The growth of individuals that settled on a 0.5 m^2 cleared surface at the high level in Cabo de Sines was measured during one year. The surface was approximately square and was cleared of all organisms in October 1991. Approximately once every two months, all macroscopic *P. pollicipes* were mapped and those with RC>4 mm were measured using callipers (precision of 0.1 mm).

The comparison of size structures across tidal levels (high and low) and shores (Cabo de Sines and Cabo Sardão) was conducted separately for juvenile barnacles attached to adult *P. pollicipes* and those attached directly to primary substratum and/or to the base of conspecifics.

For the first group, about 50 adults were collected at each date/tidal level/shore and the total number of barnacles attached per adult was counted and each individual barnacle was measured (RC) using a dissecting microscope (precision of 0.01 mm). Sampling dates were the same as the ones used in the recruitment study. For several dates, the size-frequency distribution was described.

For the second group, aggregates (or parts of aggregates) of *P. pollicipes* from each tidal level and shore were destructively sampled on several dates during 1 year. Total number of sampled animals on each occasion varied from 157 to 801. All animals were measured (RC) (using callipers and a dissecting microscope depending on individual size — precision of 0.1 mm and 0.01 mm respectively) and size-frequency distributions were analysed using size classes with 2 mm RC intervals. The first size class considered was]4,6 mm] because most animals with RC<4 mm were attached to the peduncle of conspecifics (first group). Time windows between sampling dates were similar between shores but not consistent through time (due to sea roughness), ranging from 68 to 106 days.

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In order to examine the spatial and temporal variability of the population size structure (between tidal levels and among sampling dates, respectively), a matrix of size classes × sampling dates was assembled for each tidal level and shore, and a corresponding symmetrical matrix was obtained by calculating Manhattan distances between dates using PRIMER 6 (Primer-e Ltd) according to Clarke and Warwick (2001). Manhattan distances between consecutive dates were corrected in order to get a Manhattan distance per month (MD30) for each time window. This last procedure is warranted by the lack of consistency of time windows through time; it is based on the assumption that the relationship between MD30 and time is linear.

A higher MD30 was expected with a greater change in the population structure. Variability of MD30 between tidal levels and sampling periods was tested using an analysis of variance with two fixed factors (tidal level and sampling periods) and using the two shores as the replicates. When there were significant differences ($P<0.05$), the nature of the differences was explored by SIMPER analysis (PRIMER 6, Clarke and Warwick, 2001) to detect which size-classes were more likely to drive the differences.

3. Results

3.1. Recruitment

All cypris larvae found attached to adult *P. pollicipes* were identified as *P. pollicipes* and their abundance was very low (<1% contribution to IR06). Temporal variability of recruitment (IR06) at both tidal levels and shores is shown in Fig. 2. Recruitment occurred synchronously at both tidal levels and shores with significant ($P<0.05$) correlations between tidal levels within shores (Cabo de Sines, $r=0.888$, $n=16$; Cabo Sardão, $r=0.961$, $n=11$) and between shores within tidal levels (High, $r=0.619$, $n=16$; Low, $r=0.730$, $n=11$).

Recruitment was more intense at the low tidal level and no consistent differences between shores were detected (Fig. 2 and Table 2).

Table 2
Analysis of variance on number of recruits (RC <0.6 mm) per adult *Pollicipes pollicipes* (IR06) in SW Portugal in relation to tidal level (T), shore (S) and date (D). Data transformed to $\ln(x+1)$; Cochran's test, $P>0.05$. $N=48$. SNK tests for the interaction term $T\times D$ and $S\times D$. =($P>0.05$); > or <($P<0.05$). CSi — Cabo de Sines; CSa — Cabo Sardão.

Source of variation	*df*	MS	*F*	*P*
T	1	107.36	19.32	
S	1	0.34	0.01	
D	3	42.57	36.31	
$T\times S$	1	0.018	0.01	$P>0.05$
$T\times D$	3	5.56	4.74	$P<0.05$
$S\times D$	3	34.72	29.62	$P<0.001$
$T\times S\times D$	3	2.45	2.09	$P>0.05$
Residual	752	1.17		
SNK tests				
T (D)		S(D)		
On all dates: Low>High		On two dates: CSi>CSa		
		On one date: CSi<CSa		
		On one date: CSi = CSa		

At Cabo de Sines, recruitment was intense in October 1990, and nil for the rest of the autumn-winter season (Fig. 2). In the following year, at both shores it began in July and spanned the summer, autumn and beginning of winter. In 1992, it started later into the summer (early September) than in 1991. Recruitment was never observed during the spring.

Correlations between recruitment indices were significant ($P<0.05$) at each tidal level of Cabo de Sines: High ($n=19$), IR06 versus IR1 ($r=0.941$), IR1 versus PR1 ($r=0.919$); Low ($n=17$), IR06 versus IR1 ($r=0.915$), IR1 versus PR1 (0.884). The beginning of the recruitment season is the same when using both indices (Fig. 3). However, when using the PR1 index, the drop in recruitment is smoother and the recruitment season is more prolonged than when using IR1 (Fig. 3). By comparing IR1 and PR1, it is possible to estimate that a PR1 >50% corresponded to an IR1 of >3.

At both tidal levels, recruitment was significantly lower on the capitulum and capitulum-peduncle quarter of the stalk (zones E and

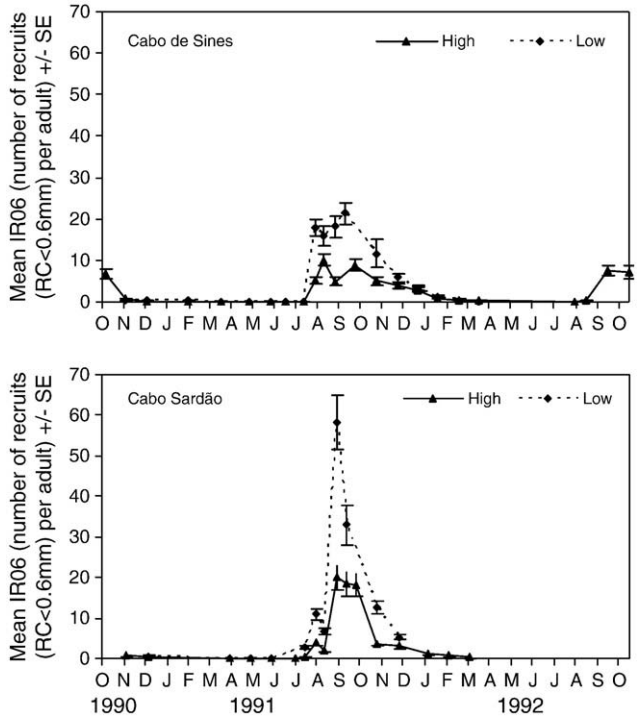

Fig. 2. Mean IR06 (number of recruits (RC <0.6 mm) per adult *Pollicipes pollicipes* ($n\sim50$)) (±SE) at two tidal levels (low and high) in Cabo de Sines and Cabo Sardão.

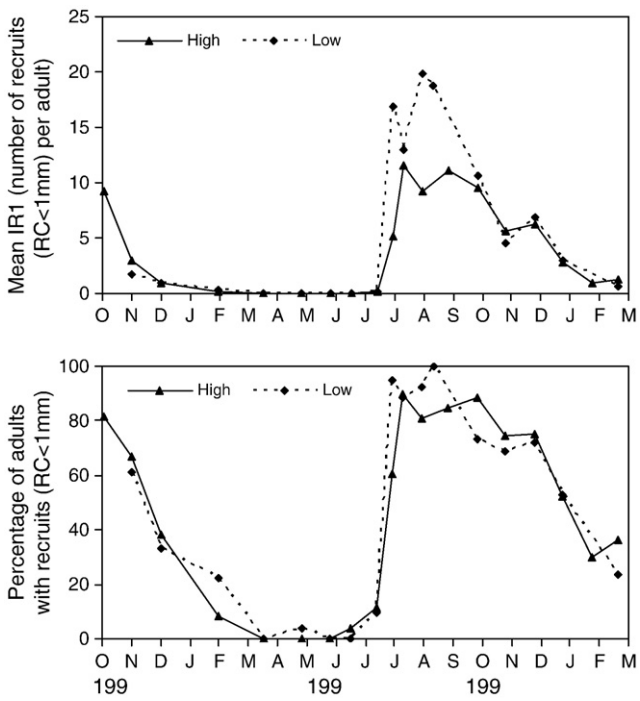

Fig. 3. Mean IR1 (number of recruits (RC <1 mm) per adult *Pollicipes pollicipes* ($n\sim50$)) and percentage of adults ($n\sim50$) with recruits (RC <1 mm) at two tidal levels (low and high) in Cabo de Sines.

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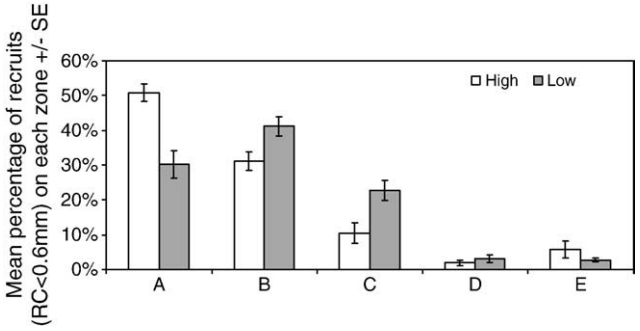

Fig. 4. Mean percentage of recruits (RC <0.6 mm) on each zone of an adult *Pollicipes pollicipes* (A, B, C, D and E — from the peduncle base to the capitulum) (±SE) at the high and low tidal levels at Cabo de Sines ($n=6$ different dates during the recruitment season of 1991; total number of recruits per date and tidal level varied from 148 to 1082).

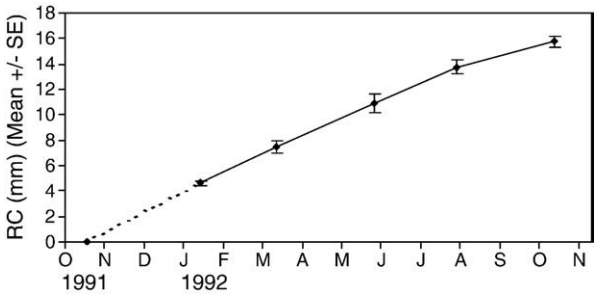

Fig. 5. Mean RC (mm)±SE of *Pollicipes pollicipes* recruited to a cleared surface of 0.5 m^2 at the mid shore in Cabo de Sines after the 25th October 1991 (clearance date). Number of measured animals varied from 5 (January), 7 (March) to 11 on the remaining dates.

D) than on the basal half of the peduncle (zones A and B) (Fig. 4, Table 3). At the high level, recruitment was more intense in zone A than in zone B, while no differences between these zones were detected at the low level (Fig. 4, Table 3).

3.2. Growth and population size structure

In January 1992, three months after clearing of all organisms from a surface of 0.5 m^2 (25th October 1991), it was possible to detect and measure five *P. pollicipes* that had settled on small pits on the surface (4.6±0.4 mm RC (mean±SD)) (Fig. 5). In October 1992, eleven barnacles with an average RC of 15.7 mm (ranging from 14.5 mm RC to 18.7 mm RC) and a maximum age of one year were found (Fig. 5). On average, these barnacles grew 1.3 mm RC per month. A slight decrease in growth was detected in the last trimester of their first year of life, from August to October.

The number of *P. pollicipes* attached to conspecifics varied substantially during the year (Fig. 6), ranging from 0 to 64 individuals per adult. The period of maximum attachment of juveniles to conspecifics was summer and autumn (average of 15 juveniles per adult), while spring was the "cleanest" season with far fewer barnacles attached to conspecifics (average of 2 juveniles per adult) (Fig. 6).

Size-frequency distributions of juveniles attached to adults taken from both tidal levels at Cabo de Sines are given in Fig. 7. The size-class of]6,9 mm RC] was always weakly represented indicating that a few barnacles within this size range remained attached to stalks of conspecifics. In contrast, the number of individuals in the first two size-classes (RC<3 mm) was highly variable and most abundant during the recruitment season (summer and autumn). There was

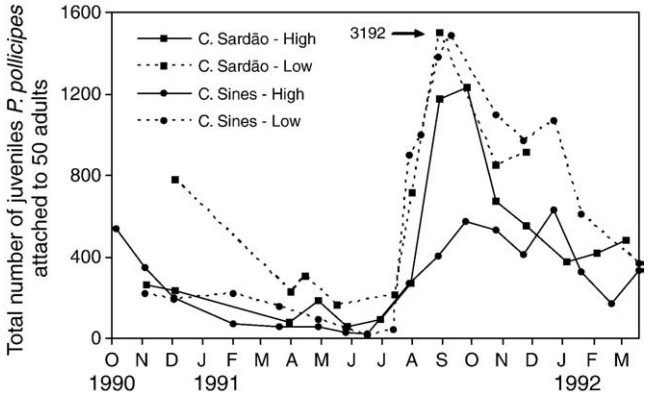

Fig. 6. Total number of juveniles *Pollicipes pollicipes* attached to 50 adults conspecifics adults at two tidal levels (Low and High) and two shores (Cabo de Sines and Cabo Sardão).

considerable inter-annual variation, as these size classes were more abundant in March 1992 than in March 1991. The shape of these size-frequency distributions was similar at both tidal levels, but a higher abundance of animals with RC<3 mm was evident at the low tidal level.

Size structures of barnacles attached to the primary substratum and/or to the base of conspecifics in both tidal levels and shores are given in Fig. 8. They were variable and ranged from bimodal (e.g. May 1991, high level, Cabo de Sines) to positively skewed distributions (e.g. May 1991, high level, Cabo Sardão), but several distributions were mixed. The largest size-class considered (RC >22 mm) was more abundant in the samples from the low tidal level than from the high level, indicating that animals can reach a larger individual size for the same age at the low shore.

The spatial and temporal variability of Manhattan distances per month (MD30) between the size-frequency distributions of Fig. 8 is shown in Fig. 9. MD30 was significantly different among sampling periods ($F=5.38$, $P<0.05$), being highest in the period from March to May. No other patterns were detected. SIMPER analyses done to compare the size-frequency distributions of March and May suggested that the main cause of change is the passage of a bimodal size structure in March to a more positively skewed distribution in May. In March, there was a first mode (~5–9 mm RC) corresponding to the previous recruitment season (animals<1 year old), and a second mode (~15–17 mm RC at the high shore; ~17 to >22 mm RC at the low shore) corresponding to animals with >1 year old. In May, there was a higher number of barnacles in the first size classes corresponding to animals that had recruited in the previous recruitment season (summer and autumn 1990). However, this pattern was not apparent at the upper

Table 3
Analysis of variance on the percentage of recruits (RC<0.6 mm) in each zone of 10 adult *Pollicipes pollicipes* in relation to factor zone (Z) and factor tidal level (T). Untransformed data; Cochran's test, $P>0.05$. $N=6$. SNK tests for the interaction term $T\times Z$. =($P>0.05$); > or <($P<0.05$). A, B, C, D and E are the five zones considered in the adult (from the peduncle base to the capitulum).

Source of variation	*df*	MS	*F*	*P*
T	1	0.05	0.5	
Z	4	0.56	53.85	
T×Z	4	0.03	2.95	$P<0.05$
Residual	50	0.01		
SNK tests				
Z (*T*)		*T*(*Z*)		
Low: A=B>C>D=E		A: Low>High		
High: A>B>C=D=E		B,C,D and E: Low=High		

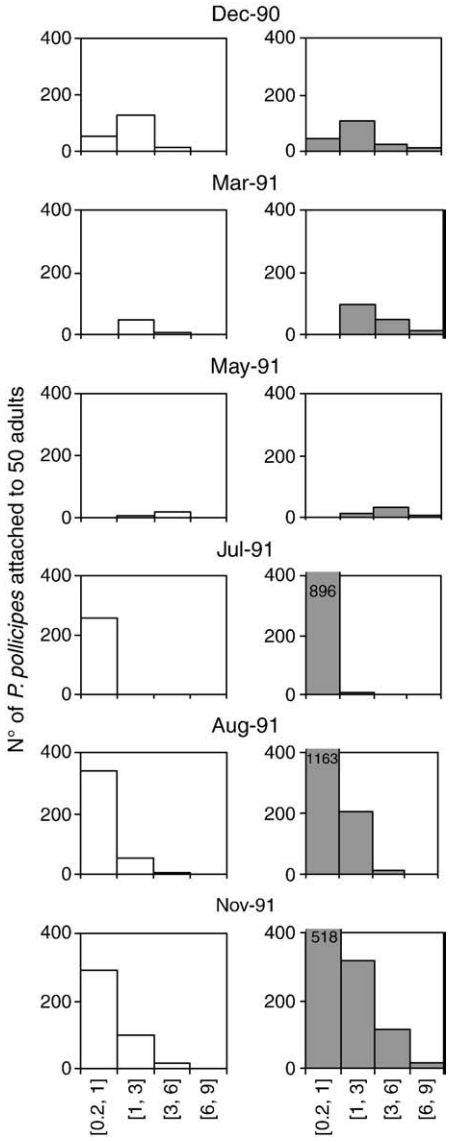

Fig. 7. Absolute size-frequency distributions of *Pollicipes pollicipes* attached to 50 adults conspecifics at two tidal levels (High — white bars; Low — grey bars) in Cabo de Sines.

tidal level of Cabo de Sines, where a bimodal distribution was still evident in May. In August, distributions were closer to a normal shape and were dominated by mid size classes (~9 to 19 mm RC). Bimodal distributions were more apparent during autumn (November) and late winter (March) than in summer (August).

4. Discussion

4.1. Recruitment

Recruitment of *P. pollicipes* on conspecifics (IR06, number of cyprids plus juveniles with RC <0.6 mm per adult) in SW Portugal was intense during summer and autumn. Abundance of cyprids was very low (<1%) and age of recruits (RC <0.6 mm) was estimated as up to two weeks. IR06 varied from 0 to 60 (number of recruits attached per adult). Considerable inter-annual variation in the timing and duration of the recruitment season was observed, but the most consistent period of recruitment was from mid-summer to mid-autumn. In 1990, the recruitment season ended in October, as IR06 was almost nil during the rest of the autumn, but in 1991, recruitment extended throughout autumn. In 1991, recruitment began in July; while in 1992 it only began in September.

Comparisons of recruitment studies made in Spain and Portugal cannot be made directly as different indices of recruitment were used: IR06 in the present study, IR1 (number of juveniles with RC <1 mm per adult) in Pavón (2003) (Asturias, N Spain); and PR1 (percentage of adults with attached juveniles with <1 mm RC) in Macho (2006) (Galicia, NW Spain). Comparisons between indices revealed that they were all positively correlated, although when using PR1, the decrease in recruitment with time is smoother and the recruitment season is apparently longer than when using IR1 or IR06. When the majority of the adult population of *P. pollicipes* at Cabo de Sines had recruits with RC <1 mm (PR1 >50%), the average number of recruits (RC <1 mm) per adult (IR1) was greater than 3. Although this relationship was not studied in Spain, when comparing two similar years (2000 and 2001) sampled in Asturias (Pavón, 2003) and Galicia (Macho, 2006), it is possible to note that during 2000, PR1 was always less than 50% (Macho, 2006) and the mean IR1 was close to or less than 3 (Pavón, 2003). During summer and autumn 2001, PR1 was higher than 50% in Galicia (Macho, 2006), and IR1 was higher than 3 in Asturias (Pavón 2003). We suggest that these values (PR1 >50% and IR1 >3) can be used to define the main recruitment season of *P. pollicipes*. Based on this definition, the main recruitment season spans summer and autumn, although considerable inter-annual variation can be observed in its timing and duration (this study), as well as its intensity (2000 versus 2001, Pavón (2003) and Macho (2006)).

P. pollicipes breeds more intensively from April to September in SW Portugal (Cruz and Hawkins, 1998; Cruz and Araújo, 1999). Very few animals carrying eggs have been observed during autumn and winter (Cruz and Araújo, 1999). Similar patterns were found by Macho (2006) in a four-year study of reproduction of *P. pollicipes* in Galicia, Spain. Correlations between sexual activity and recruitment (IR06) of *P. pollicipes* in SW Portugal were tested by Cruz (2000) using different time lags. A maximum significant and positive correlation was found at 2.5 months lag. However, larval development time of *P. pollicipes* in the laboratory is shorter (11 to 24 days, Kugele and Yule, 1996). It can be argued that there is a massive early mortality of larvae produced in the beginning of the reproductive season, as was suggested by Burrows (1988) for *Chthamalus* spp. in southern England. Low sea water temperature and availability of food, as suggested by Burrows (1988), or offshore transport of larvae are possible causes of mortality in the early reproductive season. Alternatively, larval development time of *P. pollicipes* might be longer in the ocean than when reared in the laboratory. Lucas et al. (1979) observed that laboratory-reared cyprids of *Semibalanus balanoides* could stay one month without metamorphosing and subsequently settle with success.

Inter-annual variations in the timing and intensity of recruitment of *P. pollicipes* need to be better studied in order to identify the main processes explaining this variability. Spatial correlation between shores (Cabo de Sines and Cabo Sardão, ~40 km apart) suggest that cyprids of *P. pollicipes* are being affected by the same larval pool and physical transport processes at this scale. Analyses of intra-annual variation of recruitment of *P. pollicipes* associated with the study of larval pool (e.g. behaviour, distribution and abundance of cyprids in the nearshore) and nearshore physical processes are needed in order to explain temporal variability of recruitment. In acorn barnacles, temporal variability of recruitment has been mostly associated with physical transport processes (e.g. relaxation of wind-driven upwelling (Farrell et al., 1991), internal waves and internal tidal bores (Shanks, 1986, Pineda, 1991, Ladah et al., 2005), and onshore winds (Hawkins and Hartnoll, 1982, Bertness et al., 1996).

Recruitment of *P. polymerus* in La Jolla, California, ranged from all year round but more intense during spring (IR1, Hoffman, 1989) to sporadic between late April and early August (artificial plates; Pineda, 1994), whereas in British Columbia, Canada, it occurs year round but is more intense in March, June and July (cleared quadrats, Bernard,

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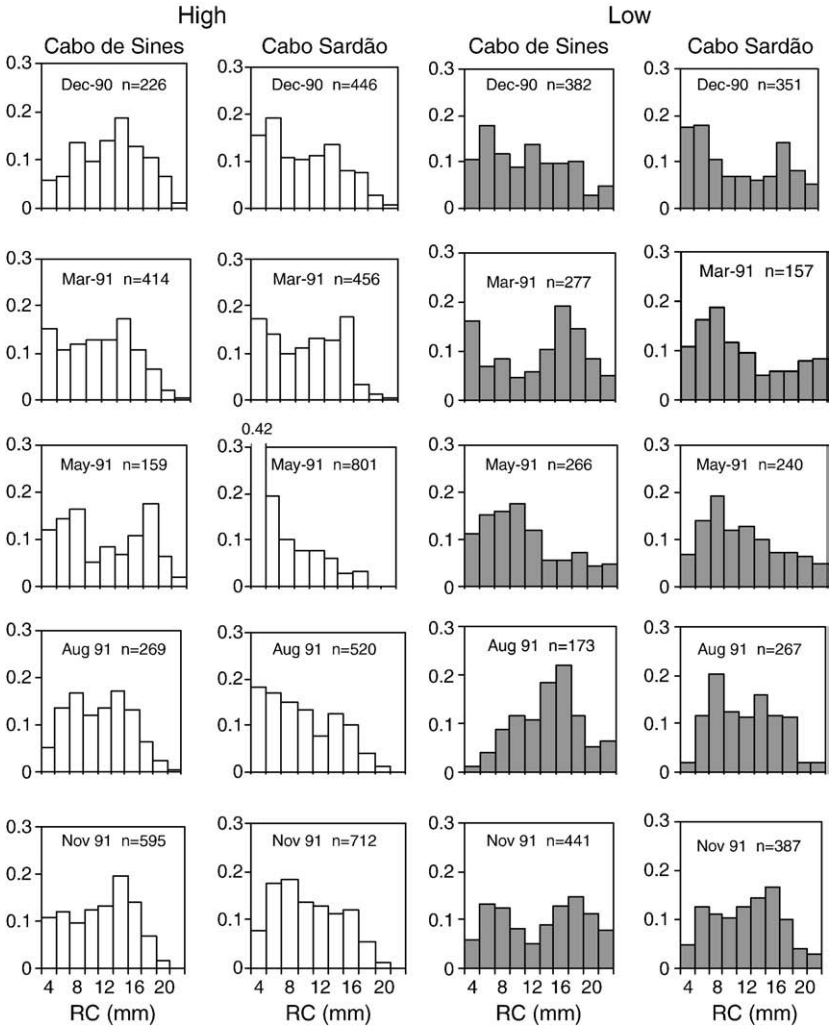

Fig. 8. Relative size-frequency distributions of *Pollicipes pollicipes* at two tidal levels (High — white bars; Low — grey bars) and two shores (Cabo de Sines and Cabo Sardão). Labels on the *X*-axis correspond to the lower limit of size classes of 2 mm (RC) interval.

1988). In contrast to SW Portugal, animals carrying eggs were observed during all of the year in California (Cimberg, 1981) and British Columbia (Bernard, 1988). Compared with the recruitment of *P. polymerus* at La Jolla observed by Hoffman (1989), recruitment of *P. pollicipes* in SW Portugal seems to be less intense, as during the main recruitment season, mean value of IR1 was about 20 in SW Portugal (both shores and tidal levels) and about 5 times higher during spring and summer in California.

While neither Hoffman (1989) nor Pineda (1994) found a consistent vertical pattern of recruitment for *P. polymerus* in California, recruitment of *P. pollicipes* in the low shore of SW Portugal was 2.5 times greater than the number of recruits in the high shore. There are several alternative explanations for this pattern in need of further investigation: 1) higher early mortality in the high shore caused by more intense predation and/or higher desiccation stress; 2) a longer period of exposure to larval availability at the low shore due to a greater immersion period; and 3) an intensification of settlement at the low shore given the lower density of adults (and consequently the area of suitable substrate) at this tidal level.

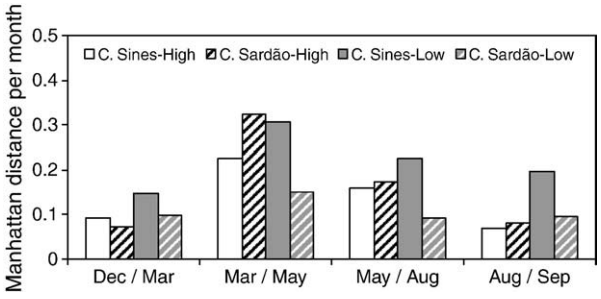

Fig. 9. Manhattan distances per month (MD30) calculated between size-frequency distributions (Fig. 8) from different dates, tide levels and shores.

The hypothesis of higher recruitment of *P. pollicipes* in the growth zone of the peduncle of conspecifics (Hoffman, 1984) was not supported, as we observed higher recruitment of *P. pollicipes* on the lower half of the peduncle. The discrepancy between patterns observed here and those found for *P. polymerus* by Hoffman (1984) might result from different early post-settlement processes in Portugal and California, from differences in cyprid behaviour between species, or from differences in the density of *Pollicipes* clumps and consequently in the availability of settlement substrate. Although there are no comparative studies on density of these species, as *P. pollicipes* is an exploited species, the density of adults within aggregates is likely to be lower in SW Portugal, when comparing with *P. polymerus* in California. In a more packed and dense aggregate of adults, the basal area of the stalks is less accessible for settlement than in less dense aggregates. A common observation in both studies was the low number of recruits attached to the capitulum. This can be explained by a higher predation

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or bulldozing by limpets on the capitulum (Hoffman, 1984, personal observations) or to a higher selectivity of cyprids for the scales of the peduncle to the detriment of the capitulum (Barnes and Reese, 1960, Chaffee and Lewis, 1988).

Although the peduncle of conspecifics could be a benign habitat for cyprids and juveniles, the number of juvenile *P. pollicipes* attached to conspecifics in SW Portugal changed dramatically through the year (from 0 to 64 juveniles per adult in average). The period of maximum attachment of juveniles to conspecifics was summer and autumn (average of 15 juveniles per adult), while spring was the "cleanest" season with fewest barnacles attached to conspecifics (average of 2 juveniles per adult). Size of juveniles attached to conspecifics was rarely greater than 6 mm (RC). These patterns can be explained by the discrete recruitment season (mainly summer and autumn), by high juvenile mortality and by a relocation of juveniles towards the host base and the primary substratum. This relocation might result from an intense intraspecific competition of juvenile *P. pollicipes* attached to conspecifics. Active relocation of *P. pollicipes* towards the base of the peduncle has been observed by Kugele and Yule (1993, 2000).

4.2. Growth and size structure

Individual growth rates of *P. pollicipes* on a denuded surface measured over one year showed that barnacles with a maximum age of one year reach an average size of 15.7 mm (RC), which corresponds to an increment of 1.3 mm RC per month. Animals with RC > 12.5 mm were sexually mature for both sexes (Cruz and Araújo, 1999). With respect to *P. pollicipes*, no other studies have measured growth in aged animals. Cruz (2000, reanalysing data presented by Cruz, 1993) has measured growth of *P. pollicipes* juveniles (RC < 10 mm) and adults (RC > 10 mm) of unknown age in three months periods and observed the following rates: 0.3 to 9.1 mm RC per year, in adults; 0.5 to 12.3 mm RC per year, in juveniles. On average, juveniles grew 0.47 mm RC per month (in three periods — winter, spring and summer), while adults grew 0.47 mm RC per month (in winter and spring) and 0.11 mm RC in summer. These growth rates are lower and more variable than those found in the present study with aged animals. These differences in growth estimates between aged and un-aged animals can be due to a higher growth during the first year of life and to the possibility that un-aged animals can be > 1 year old. Additionally, the higher growth rates measured in the present study can result from a lower intra and interspecific competition pressure upon the animals that have settled on a cleared surface when compared with animals that live and grow within an aggregate, as the ones measured by Cruz (1993, 2000).

Barnes (1996) has extensively reviewed the growth studies of *P. polymerus* and a high variability was also found (RC): 11 to 15 mm in the first year (intertidal, San Juan Island, USA, Lewis and Chia, 1981); 15 mm in the first year (intertidal, Vancouver Island, Canada, Bernard, 1988); 18 mm in the first year (intertidal, San Juan Island, USA, Paine, 1974; intertidal, Santa Barbara, USA, Page, 1986); 30 mm in the first year (oil platform, off Santa Barbara, USA, Page 1986); mean of 5.5 mm in 47 days for juveniles with a maximum of 11 mm (intake sea-water system of Scripps Institution of Oceanography, USA, Hoffman, 1988); 9 mm in one month for juveniles (under surface of rock in continuous immersion, La Jolla, USA, Hoffman, 1989). Growth estimates with un-aged *P. polymerus* were also lower (RC): 1 to 2 mm per year for animals with RC > 13 mm; 0.5 to 0.7 mm in 16 months for animals with RC > 17 mm (Barnes and Reese 1960). To our knowledge, no more recent studies about growth of *Pollicipes* are available. Patterns and processes of growth of *Pollicipes* namely *P. pollicipes* need to be better studied.

Size structure analyses of *P. pollicipes* attached directly to primary substratum and/or to the base of conspecifics evidenced that barnacles at the low tide level reached a higher maximum size which can indicate that growth at this tidal level was higher than at the high shore. In the reviewed studies described above, the vertical variation in growth was not analysed.

A higher temporal variability between size-frequency distributions was detected in spring (March to May) associated with the passage from a bimodal size structure in March to a more positively skewed distribution in May. In March, there was a first mode (~5–9 mm RC) corresponding to the previous recruitment season (animals <1 year old), and a second mode (~15–17 mm RC at the high shore; ~17 to >22 mm RC at the low shore) corresponding to animals with >1 year old. In May, there was a greater number of barnacles in the first size-classes corresponding to animals that had recruited in the previous recruitment season (summer and autumn 1990). In August, distributions were closer to a normal shape and were dominated by mid size classes (~9 to 19 mm RC). Consequently, it was impossible to follow a cohort during its entire first year after settlement, as by May and during summer, in general, animals with less than 1 year old are well mixed with older animals in terms of their sizes. This could be due to the potentially long duration of the recruitment season (e.g. summer and autumn), to a higher growth rate during the first year of life as suggested above, and to an accentuated decrease in growth after the

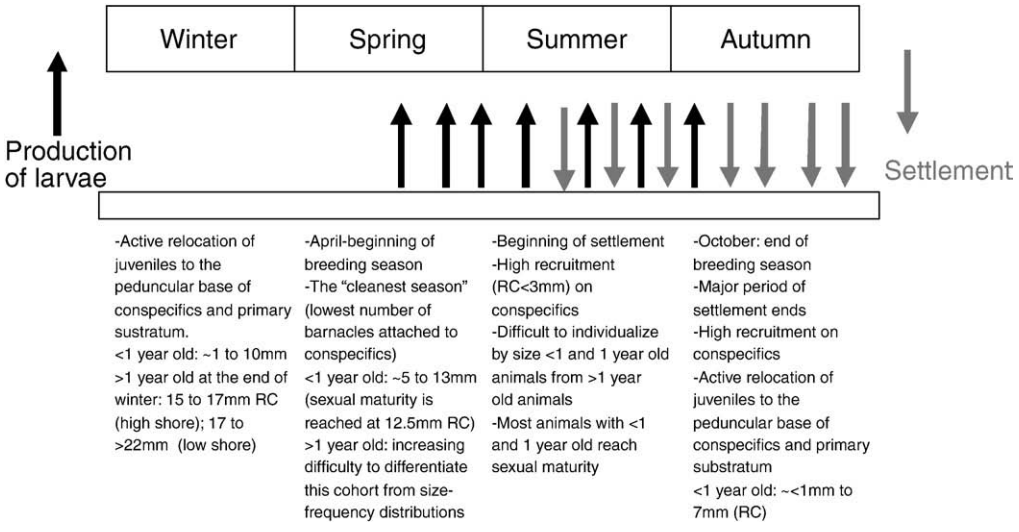

Fig. 10. Life cycle model for *P. pollicipes* in SW Portugal based on the present study and on Cruz (2000) and Cruz and Araújo (1999). Size variable is RC.

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first year. Additionally, as this species is commercially exploited, it might be difficult using size-frequency distributions to track older cohorts that presumably include the larger and most exploited animals.

During autumn (November) and late winter (March), bimodal distributions were more apparent. The first mode (~5 to 7 mm RC) should be the result of the recruitment season that begun during summer and of the active relocation of barnacles towards the base of the host and the primary substratum.

Finally, based on the present study and on information from Cruz (2000) and Cruz and Araújo (1999), we propose a general model for the life cycle of *P. pollicipes* in SW Portugal that is illustrated in Fig. 10. As *P. pollicipes* is intensively and commercially exploited, this model has implications for the management of this species: the period from mid-summer to the beginning of autumn is biologically critical for this species as it is very important for reproduction and recruitment; spring is the less sensitive period in terms of juvenile mortality directly caused by human harvesting as it corresponds to the "cleanest season", although this period is also important for reproduction and production of larvae; animals can reach an adult commercial size ($\geq$20 mm RC, namely in the low shore) one year after settlement.

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